Proceedings of the United States National Museum

SMITHSONIAN INSTITUTION • WASHINGTON, D.C.

Volume 123 1967 Number 3607

DETROIT PUBLIC LIBRARY

JUN 28 1967

TECHNOLOGY & SCIENCE

The Role of the Depressor Mandibulae Muscle In Kinesis of the Avian Skull

By Richard Zusi

SMITHSONIAN PRESS

Proceedings of
the United States
National Museum

SMITHSONIAN INSTITUTION • WASHINGTON, D.C.

Volume 123 1967 Number 3607

The Role of the Depressor Mandibulae Muscle in Kinesis of the Avian Skull

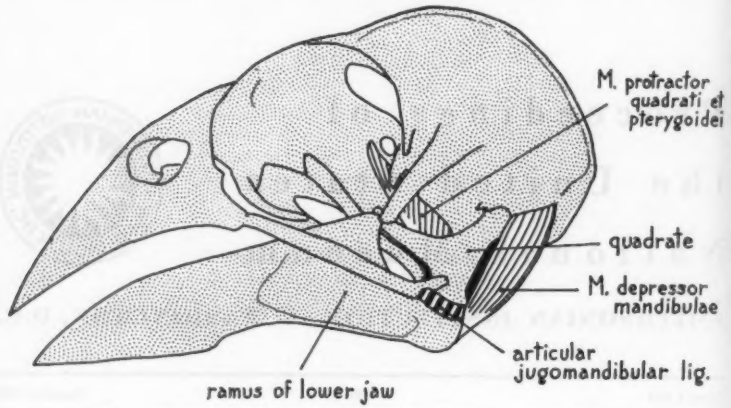
By Richard Zusi

Associate Curator, Division of Birds

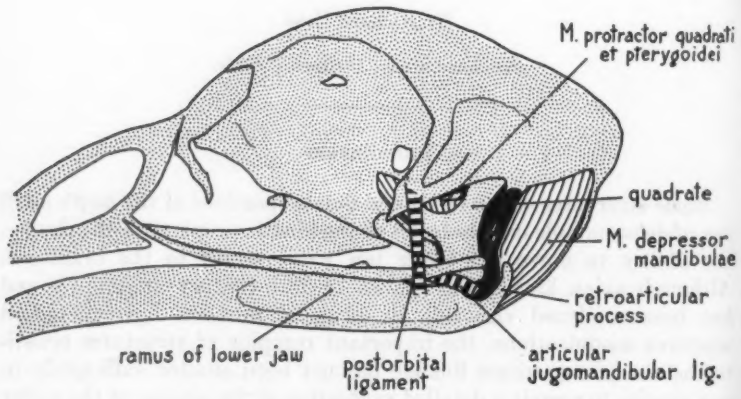
Introduction

Basic structures of the facial and palatal portions of the bird's skull are understandable only in terms of the kinetic property of the skull—the ability to move the upper jaw with respect to the braincase. Although avian kinesis was known to 18th-century anatomists and has been analyzed variously in terms of muscles, ligaments, and adaptive modifications, the important complex of structures constituting the jaw-quadrate linkage has not been studied sufficiently in any species to permit a detailed evaluation of the actions of the major jaw muscles.

My purpose here is to examine a single muscle, *M. depressor mandibulae*, to determine the effects upon jaw action of variations in muscle configuration and variations in the jaw articulation through which the muscle acts. (See fig. 1 for structures under discussion in this paper.) My methods include experiments based on stimulation of muscles in live birds, construction of models of the muscle-ligament system, and manipulation of fresh and preserved specimens. The



Hesperiphona vespertina



Gallus domesticus

FIGURE 1.—Structural features of the head in the evening grosbeak (*Hesperiphona vespertina*) and domestic chicken (*Gallus domesticus*). (Adductor and retractor muscle groups removed.)

most commonly stated action of *M. depressor mandibulae* is to open the lower jaw, but emphasis herein will be placed on the interaction between the postorbital ligament and the depressor mandibulae in protraction (raising) of the upper jaw. Several authors have postulated such a protraction effect through the postorbital ligament (Kripp, 1933, pp. 556–559; Starck, 1940, pp. 618–620; Barnikol, 1952, pp. 382–384; Zusi, 1962, p. 47; Bock, 1964, pp. 19–22), explaining its action, with some variations, as follows: the ligament is a virtually unstretchable band running from the cranium to the mandible and attaching anterior to the quadrate articulation, where the ligament provides a fulcrum around which the lower jaw pivots (see fig. 2). The depressor mandibulae rotates that portion of the lower jaw lying

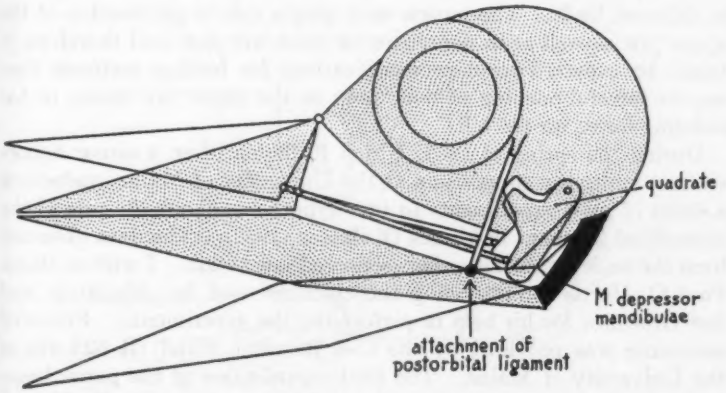


FIGURE 2.—Diagram of protraction of the upper jaw through the depressor mandibulae and postorbital ligament. The lower jaw pivots about the attachment of the ligament. As the lower jaw opens, the quadrate is pushed forward and the upper jaw is raised.

behind the attachment upward and forward, rocking the quadrates forward and thereby protracting the upper jaw. The important point is that the lower jaw pivots about the ligamentary attachment rather than about the quadrate articulation as is commonly stated. Bock (1964) has explored the significance of the postorbital ligament and has presented a number of hypotheses about avian kinesis that will be discussed below.

The group of structures that support the lower jaw form a closely interacting functional complex that is part of the larger complex of the entire kinetic mechanism. The support system includes the quadrate, the rami of the lower jaw, the jaw-quadrate articulation, and the muscles and ligaments associated with these structures. Most of the jaw muscles have the potential for moving the quadrate either through

direct attachment or indirectly by spanning its cranial and mandibular articulations. Motion of the quadrates has a direct effect on motion of the upper jaw and on the lower jaw as well; motion of the lower jaw may in turn induce shifting of the quadrates through features of the jaw articulation and ligaments. Understanding the functional properties of the complex kinetic mechanism is thus very difficult, but it is essential for the interpretation of variation of these structures in birds.

The depressor mandibulae has considerable potential for evolutionary development of functional-anatomical variation. Because of its superficial position, its origin may expand posteriorly over the neck muscles or dorsally and anteriorly over the skull and adductor muscles providing variation in both size and angle of pull of the muscle in different birds. The muscle may play a role in protraction of the upper jaw as well as in depression of the lower jaw, and therefore, it might be expected to show modifications for feeding methods that require forceful opening of both jaws or the upper jaw alone, or for resisting forces on the bill.

During the spring of 1963, Ulrich Kalkofen, then a senior honors student under my supervision at the University of Maine, undertook a series of pilot experiments to test hypotheses about the role of the postorbital ligament in kinesis (Kalkofen, 1963). The data obtained form the basis for the following section on jaw action. I wish to thank Paul C. Harris for providing the chickens used for this study and Jon Greenlaw for his help in performing the experiments. Financial assistance was provided by the Coe Research Fund (R 625–49) of the University of Maine. The final organization of the paper benefited greatly from the constructive criticisms of George E. Watson and Paul Slud. I am indebted to Walter J. Bock for providing me with a translation of the 1958 paper by Yudin.

Experiments on Jaw Action

METHODS.—Live birds used for experiment were the evening grosbeak (*Hesperiphona vespertina*) and the domestic chicken (*Gallus domesticus*)—hens of parentage female barred Plymouth Rock × male Rhode Island red. These species were especially suitable because they were readily obtainable and easily kept in captivity, and because the postorbital ligament is poorly developed in the grosbeak and strongly developed in the chicken.

For each species a wooden head support was constructed to conform with the contour of the mid-dorsal surface of the cranium; each support was held rigidly in place by metal clamps that penetrated under the supraorbital rims of the skull. Birds were first weighed

and then anaesthetized by intramuscular injection of equitheesin (0.20 ml. per 100 grams body weight, or more if necessary). Great care was taken to ensure that the birds were anaesthetized completely before and during the experimentation. Feathers of the head and neck were trimmed and the skin of both sides of the head reflected as soon as the bird lost consciousness. After the head support was fastened firmly to the bird, the support was held motionless by a vise and the body of the bird supported by the table or horizontally suspended in a plastic tube (fig. 3). The exposed jaw muscles were kept moist and clean throughout the experiments by periodic flushing with avian Ringer's solution at 38° C. The depressor mandibulae muscles were caused to contract simultaneously by a tetanizing

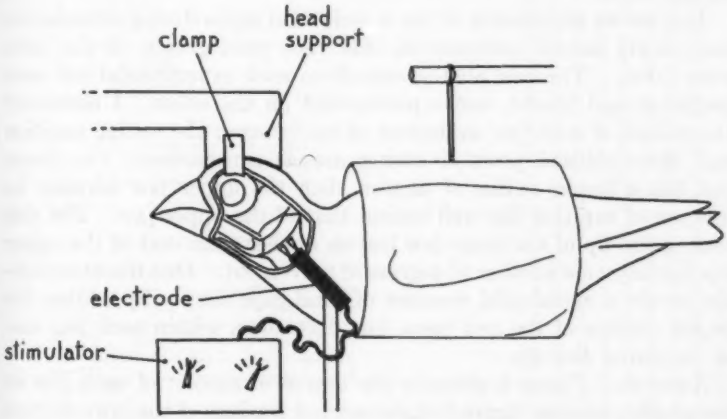


FIGURE 3.—Diagram of experimental setup for stimulating the depressor mandibulae muscles. The bill was photographed as viewed in the diagram before and during muscle stimulation.

stimulus of 20 volts (using two Harvard apparatus stimulators) applied through electrodes. The tips of both copper wires of each electrode were fitted with platinum wire bent as a triangle with one point of the triangle soldered to the wire and the opposite side of the triangle placed against the surface of the muscle. The bases of the two triangles of each electrode were parallel, about three mm apart, and were placed perpendicular to the long axis of the muscle. This type of contact gave consistent contractions, was easily applied and adjusted, and caused no damage to the muscles. Before stimulating the muscles simultaneously, each was individually stimulated to see that both were performing in a similar manner. Only at voltages exceeding 50 (and especially approaching 100) were there

spasmodic and unpredictable motions of the jaws caused by contractions of other muscles. Although 20 volts probably did not produce maximum contraction of the depressor mandibulae, it produced consistent jaw motions that could be safely attributed to contraction of the muscle under study.

The maximum number of consecutive stimulations, each of which lasted about two seconds, was 18 for a grosbeak and 17 for a chicken, during which the depressor muscles showed no signs of fatigue. Despite extensive severing of other jaw muscles the birds continued to respond well. All birds were killed while still under anaesthesia. The nature and extent of the operative procedures were then checked under a dissecting microscope immediately following each experimental series.

Just before stimulation of the muscles and again during stimulation and steady tetanic contraction, side view photographs of the jaws were taken. The two photographs from each experimental set were projected and traced, one superimposed on the other. I measured the motion of each jaw as degrees of arc between the resting position and the stabilized position during muscle contraction. The lower jaw has a longer radius of motion than the upper jaw because its fulcrum of rotation lies well behind that of the upper jaw. For this reason, the tip of the lower jaw travels farther than that of the upper jaw for the same number of degrees of movement. One therefore cannot obtain a meaningful measure of total gape simply by adding the degree motion of the two jaws, but differences within each jaw can be compared directly.

RESULTS.—Figure 4 presents the degree of motion of each jaw in bar graphs, whereas figure 5 shows several tracings of the jaws to give the reader a better impression of the actual amount of jaw motion. I must emphasize that throughout the experiments the depressors probably never were contracted maximally and the major protractor muscle of the upper jaw (protractor quadrati et pterygoidei) did not contribute to the observed jaw motion. As stated before, the evening grosbeak lacks a well-defined postorbital ligament, whereas the domestic chicken has a stout one.

It is clearly indicated in figure 4 that muscle contractions in the chicken produced repeatable results during experimentation with each bird (see A 1 and 2, 4 and 7; C 1 and 2; D 4 and 6, 7 and 9) and comparable results between different birds treated on different days (A 1, B 1, C 1, D 5).

The results of the experiments may be summarized as follows: (1) the depressor mandibulae caused protraction (raising) of the upper jaw and depression of the lower jaw in the domestic chicken and evening grosbeak; (2) the muscle caused opening of both jaws in the

FIGURE 4.—Bar graphs of jaw motions during muscle experiments. Vertical axis equals degree of motion of each jaw measured above and below 0° (the closed position of both jaws). In each bar, the end closest to the 0° line shows the position of the jaw before contraction of the depressor mandibulae; the opposite end of each bar shows the position of the jaw during contraction. (A through F = different birds; numbers above bars = different experiments; number within a bar = consecutive position of that experiment in total experimental series; n = normal bird; 5g, 10g = gram weights suspended from culmen; po. = postorbital ligaments were cut; add. po. = all adductor muscles and postorbital ligaments were cut; △ = restriction of jaw motion at apex of triangle.)

chicken after removal of the postorbital ligament; (3) protraction of the upper jaw by the depressor mandibulae was reduced after removal of the postorbital ligaments in the chicken; (4) depression of the lower jaw occurred when the upper jaw was held closed in both species; (5) protraction of the upper jaw occurred when the lower jaw was held closed in both species; and (6) the postorbital ligament played a role in holding the lower jaw partially closed at rest. In addition, protraction in the chicken following removal of the postorbital ligament was about half that of the normal condition. A weight of ten grams suspended from midway along the exposed culmen of the chicken reduced protraction in the normal bird and prevented protraction in birds from which the postorbital ligaments had been removed. Limiting or preventing motion of one jaw reduced but did not prevent motion of the other jaw. The postorbital ligament alone did not hold the lower jaw completely closed at rest (see fig. 4: A 1, 2, 3), but removal of the ligament shifted the jaw to a more depressed resting position. That the adductor muscles also played some role in support of the resting jaw is suggested by B 3, in which the jaw at rest was most strongly depressed following removal of both the postorbital ligaments and adductor muscles.

DISCUSSION.—The fact that the postorbital ligament and the depressor mandibulae can together produce protraction of the upper jaw is demonstrated by the experiments on domestic chickens described above. The ligament thus serves to coordinate motions of both jaws during depression of the lower jaw. Coordination of both jaws through the depressor mandibulae, however, does not require the presence of the postorbital ligament, and the ligament must be regarded as only one of several means (excluding other jaw muscles) of producing coordination. Furthermore, coordination of the jaws in the presence of a postorbital ligament is not obligatory; either jaw may also be moved independently.

Bock (1964) discussed the role of the postorbital ligament in avian kinesis, basing his conclusions on the results of manipulation of jaws in fresh birds and on inference from the anatomical structure of the jaw mechanism. His major hypotheses were as follows: (1) Two basically different kinetic mechanisms exist in birds—*coupled* and *uncoupled*. The jaws are coupled in those species with a postorbital ligament (or a functionally equivalent ligament), and/or with an interlocking arrangement of the jaw-quadrate articulation. Birds lacking both of these features have uncoupled jaws. (2) When the upper jaw of a coupled bird is held firmly in place, the lower jaw cannot be depressed. (3) In uncoupled birds the depressor mandibulae does not contribute to raising the upper jaw except perhaps when the mandible is depressed against resistance. (4) In coupled kinesis

it is impossible to depress the upper jaw beyond the closed position. (5) The elevated upper jaw cannot be lowered without raising the mandible. (6) Only those few groups of modern birds having uncoupled kinesis could have given rise to an akinetic form.

Although the experiments confirm the existence of coordinated jaw motion through the postorbital ligament, they nevertheless contradict

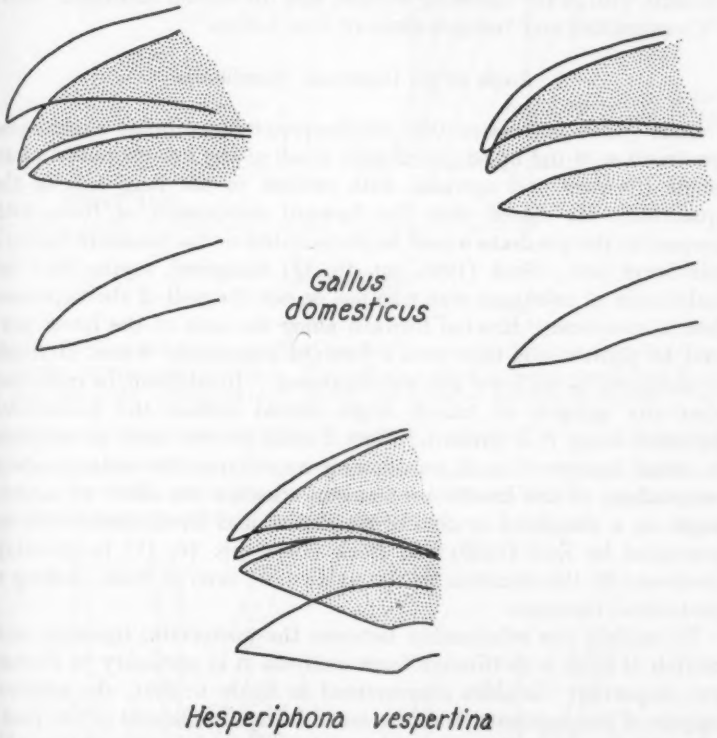


FIGURE 5.—Tracings of jaws from superimposed photographs taken before (stippled) and during contraction of the depressor mandibulae muscles. (Left: normal bird; middle: normal bird; right: postorbital ligaments cut. Drawings do not present maximum opening of either jaw.)

Bock's assumptions 1, 2, and 3 directly and 4, 5, and 6 by implication. The avian kinetic mechanism should not be regarded as either strictly coupled or uncoupled; rather, it is likely that many birds are coupled weakly, but probably few are coupled so strongly that other muscles cannot counteract the jaw linkage. Approaches toward complete coupling or complete independence of jaw action would represent

special adaptions rather than typical conditions. To better understand these complex kinetic relationships, three main questions must be answered: (1) How does the postorbital ligament produce coordination of the two jaws? (2) How can the jaws be alternately "coupled" and "uncoupled"? (3) What factors produce coordination in addition to or in the absence of the postorbital ligament? The first question is dealt with in the following section, and the second and third, under "Coordination and Independence of Jaw Action."

Angle of the Depressor Mandibulae

Zusi (1959) postulated that the depressor mandibulae could cause protraction of the upper jaw if part or all of the muscle pulled at an angle (forward and upward) with respect to the long axis of the quadrate. He stated that the forward component of force with respect to the quadrate would be transmitted to the quadrate through the lower jaw. Bock (1964, pp. 16, 17) disagreed, saying that the only point of relevance was whether or not the pull of the depressor had a component directed forward along the axis of the lower jaw, and he pointed out that such a forward component would diminish or disappear as the lower jaw was depressed. In addition, he indicated that any analysis of muscle angle should include the postorbital ligament when it is present. Here I shall present such an analysis in detail because it is of considerable importance for understanding adaptations of the kinetic mechanism, whereas the effect of muscle angle on a simplified system of weightless and frictionless levers as presented by Zusi (1959) and Bock (1964, pp. 16, 17) is probably irrelevant to the situation in the avian jaw, even in birds lacking a postorbital ligament.

To explain the relationship between the postorbital ligament and motion of both jaws through force analysis, it is necessary to discuss two important variables diagrammed in figure 6: first, the relative lengths of the segments from the mandibular attachment of the postorbital ligament to the center of rotation of the jaw articulation (A) and from the ligament's attachment to the insertion of the depressor mandibulae (B); and second, the angle of the depressor mandibulae in relation to its neutral axis. The force of the depressor mandibulae (F) can be replaced by two components, H and V, running in line with and vertical to the force arm B. To determine the effect of these components on the quadrate, one must transfer both components, H′ and V′, to the jaw-quadrate articulation. The clockwise rotational component V′ is increased by the amount $V' = \frac{V \times B}{A}$ whereas the counterclockwise component H′ remains the same, and

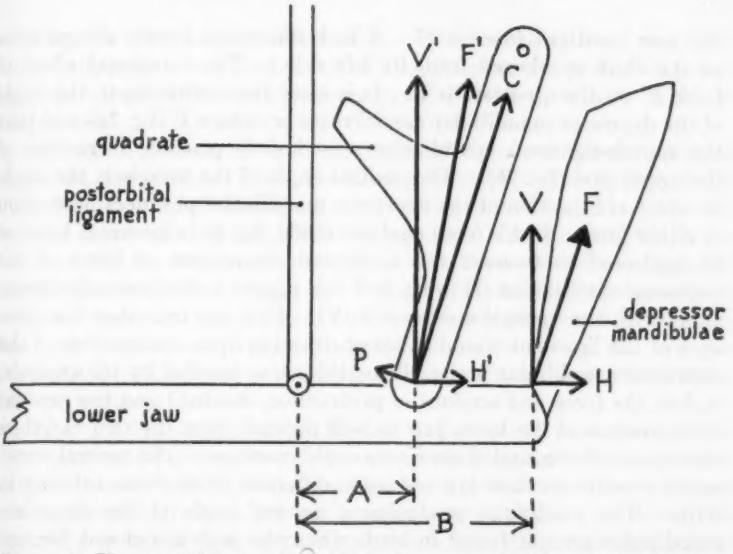


FIGURE 6.—Diagram of forces produced by the depressor mandibulae in a simplified supporting system of the lower jaw. (F=resultant force of depressor mandibulae; V and H=rectangular components of F; H'=H transferred to quadrate articulation; V'=V transferred to quadrate articulation and increased in relation $V'=\frac{V\times B}{A}$; F'=resultant of components V' and H'; P and C=rectangular components of F'; A=work arm from fulcrum at attachment of postorbital ligament to quadrate; B=force arm from postorbital ligament to insertion of depressor mandibulae.)

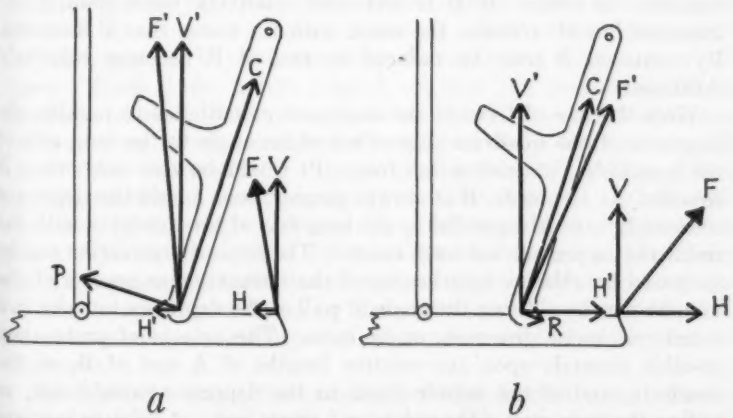


FIGURE 7.—Effect of the angle of the depressor mandibulae upon motion of the upper jaw through the postorbital ligaments: *a*, protraction force P increased by counterclockwise shift of F (compare with fig. 6); *b*, retraction component R produced by clockwise shift of F (compare with fig. 6). (Symbols defined in fig. 6.)

the new resultant force is F′. (Clock directions herein always refer to the skull as viewed from its left side.) The rotational effect of force F′ on the quadrate is P. It is clear that variation in the angle of the depressor mandibulae can increase or reduce P (fig. 7*a*) and that the muscle-ligament combination could even produce retraction of the upper jaw (fig. 7*b*). The neutral angle of the muscle is the angle at which contraction of the depressor mandibulae produces no motion of either jaw. Bock's force analysis (1964, fig. 9) is incorrect because he neglected to transfer the backward component of force of the depressor mandibulae (H in fig. 6 of this paper) to the jaw articulation along with the upward component (V). It is not true that the presence of the ligament would cause protraction upon contraction of the depressor mandibulae under all conditions, as implied by his analysis; rather, the force and amount of protraction obtained and the amount of depression of the lower jaw as well depend upon the two variables mentioned above, and these forces could reach zero (the neutral state) under conditions that are not very different from those existing in birds. The conditions producing a neutral angle of the depressor mandibulae are not found in birds when the jaws are closed because such conditions would prevent opening of *both* jaws. Birds in which the geometry of the jaw-support system departs most strongly from a neutral arrangement probably represent special adaptations for coordination of the jaws through the depressor mandibulae.

Just as components V′ and H′ are altered by variations in the angle of F, their effect upon protraction varies with changes in the relative lengths of the force and work arms (B and A) when the muscle angle remains the same. If B is increased relatively more than A, V′ increases but H′ remains the same, with the result that P increases. By contrast, P may be reduced to zero if B becomes relatively shortened.

Were the line of force of the depressor mandibulae to parallel the long axis of the quadrate (regardless of its angle to the long axis of the mandible), its protraction force (P) would be zero only when B equalled A. In birds, B is always greater than A and the depressor commonly is nearly parallel to the long axis of the quadrate with the result that a protraction force exists. The *force* of protraction can be increased by relative lengthening of the retroarticular process of the mandible or by shifting the angle of pull of the depressor muscles in a counterclockwise direction, or by both. The *amount* of protraction possible depends upon the relative lengths of A and of B, of the quadrate, and of the muscle fibers in the depressor mandibulae, as well as the geometry of the palate and upper jaw. A relative increase in A with respect to B would increase the degree of protraction with a given contraction of the depressor muscles, at the same time re-

ducing the force of protraction. The attachment point of the postorbital ligament, however, is never far in front of the jaw articulation as this would reduce the amount by which the lower jaw could be depressed.

During depression of the lower jaw by the depressor mandibulae muscles, the resultant force of each depressor muscle shifts in a clockwise direction relative to the bones. It is possible that the geometry of the entire ligamentary mechanism is such that, in some birds, the system reaches a neutral condition before the mandible is depressed to the limits allowed by the jaw articulation alone. Full contraction of the depressor mandibulae thus would stabilize both jaws in an opened position without permitting excessive strain on the jaw articulation or kinetic articulations that might occur in the absence of the ligament.

Zusi (1959) postulated that birds that force their jaws open against environmental resistance (probers, gapers) may derive a protraction effect through the depressor mandibulae in that the point of resistance to depression of the lower jaw creates a new fulcrum, replacing that of the postorbital ligament. (In figure 6, A and B would then extend from the point of resistance near the tip of the jaw to the quadrate and to the depressor mandibulae, respectively.) In the light of the above analysis, it is clear that the mechanism would work effectively only if F were shifted in a counterclockwise direction to offset the loss of protraction force incurred by the relative increase in the ratio of A to B, or if the ratio were reduced by elongation of the retroarticular process of the mandible. I have not carried the analysis for any particular species far enough to be able to say whether or not the depressor mandibulae alone could produce protraction of the upper jaw in the presence of environmental resistance on both jaws. Bock (1964, p. 17) pointed out that the analysis is difficult and must include both jaws. It seems likely, however, that species with a strong forward component to the pull of the depressor mandibulae would be capable of stronger gaping (forceful opening of both jaws), not only by increasing the force of depression of the mandible, but also by favoring conditions for protraction of the upper jaw as well. The validity of the difference between the adaptations found in the depressor mandibulae muscles of *Sturnus vulgaris* and gapers of the Icteridae postulated by Zusi (1959) is thus strengthened by the above analysis although the explanation originally proposed was incorrect.

In species lacking a functional postorbital ligament, any structure that resists depression of the lower jaw will cause protraction of the upper jaw through forces similar to those diagrammed in figure 6 but only in proportion to the amount of resistance offered by the structure.

The large adductor muscles of the jaw, and in particular *M. pseudotemporalis superficialis*, which in many species lies in a position comparable to that of the postorbital ligament but medial to it, may serve this function in a passive manner. The pseudotemporalis superficialis, often highly tendinous, might functionally replace the ligament by active contraction as well. There is clearly a great need for experimental approaches to the problems of avian kinesis to test the important specific questions that now can be asked.

Although the effect of muscle angle on protraction of the upper jaw in the absence of any restraining forces anterior to the jaw articulation

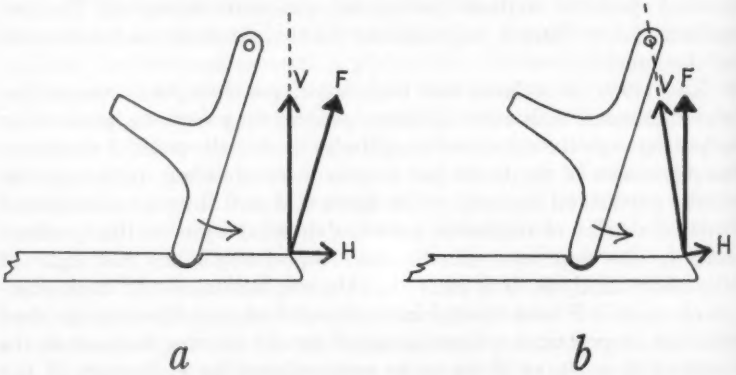


FIGURE 8.—Diagram of forces on the lower jaw and quadrate from the depressor mandibulae in the absence of the postorbital ligament: *a*, with unrestricted rotation of the lower jaw, H serves to retract the quadrate and V serves primarily to rotate the lower jaw (H reaches zero when F is perpendicular to the lower jaw); *b*, with reduction or loss of rotation at the jaw articulation, H retracts the jaw-quadrate unit and V has no rotational effect (H reaches zero when F passes through the otic articulation of the quadrate). (F=resultant force of depressor mandibulae; H and V=rectangular components of F; curved arrows=motion of quadrates under conditions illustrated.)

probably seldom has a bearing on jaw motion in birds, I shall discuss it briefly because it has been mentioned in the literature. If the struts and hinges of the model shown in figure 8*a* were weightless and frictionless, the effect of muscle angle would probably be that described by Bock (1964, p. 17)—that is, protraction or retraction would depend only on the muscle's pull forward or backward from a 90-degree angle (the neutral angle) to the mandible. Were there friction or any other resistance to rotation at the jaw-quadrate hinge, protraction would occur if the line of pull of the muscle passed ahead of the cranial articulation of the quadrate and retraction would occur if it passed behind the articulation (fig. 8*b*). The neutral angle would

pass through the cranial articulation. In the most common circumstances there is some form of resistance to depression of the mandible anterior to its articulation, and the line of pull of the depressor then has relevance for protraction only if it angles forward from the neutral angle, which is determined by the geometry of the whole system as already explained. In any case, an evolutionary shift in the direction of pull of the depressor mandibulae in a counterclockwise direction represents a functional change along the continuum "retraction—neutral—protraction" with respect to the muscle's influence on the upper jaw.

Coordination and Independence of Jaw Action

POSTORBITAL LIGAMENT.—Coordination of the jaws through the postorbital ligament (or its functional equivalent, as in the lacrymomandibular ligament in certain ducks) requires that the ligament attach on the mandible anterior to the jaw articulation. Should the ligamentary attachment approach the jaw articulation (or should A in figure 6 be reduced) the amount of protraction obtained through the ligament would be correspondingly reduced. Coordination would reach zero when the ligamentary attachment lay opposite the jaw articulation. By manipulation of the jaws of fresh specimens of the sooty tern (*Sterna fuscata*), I found that a pull on the depressor muscles caused very little forward or backward displacement, relative to the braincase, of the postorbital ligament and lower jaw during depression of the jaw; instead, the quadrate was displaced forward and the upper jaw raised. On the other hand, when motion of the upper jaw was restricted and the quadrates thereby held stationary, depression of the lower jaw was accompanied by a backward shift of the lower jaw and postorbital ligament relative to the braincase and quadrates. (Strict limits to this backward shift were set by the articular jugomandibular ligament.) Whether the jaw shifts backward or the quadrate forward, the shift is enough to bring the attachment point of the postorbital ligament closer to the rotation center of the jaw articulation and to reduce the coordinating action of the ligament. (Manipulation of the jaws was accomplished through pulling on the depressor mandibulae muscles or by applying pressure on the jaw at their points of insertion. Manipulation of the jaws by their tips may give different results that do not correspond to actions of the depressor mandibulae muscles.)

The ability of the lower jaw to shift backward with respect to the quadrate may be deduced from the jaw motions of an evening grosbeak that is hulling sunflower seeds. The bird moves its lower jaw to the right or left of the upper jaw to facilitate manipulation of the seeds.

Because the two quadrates are held in comparable positions by the jugal and palatal struts and therefore cannot move independently, one of the mandibular rami must slide backward along the quadrate while the other remains in place during displacement of the jaw to the side. The possibility of backward displacement of the lower jaw in the domestic chicken, although less obvious during normal feeding of the bird, can be demonstrated by manipulation of fresh heads. I conclude that the shift of the ligamentary fulcrum toward the jaw articulation is one means of overcoming strict "coupling" by the postorbital ligament.

In addition to the experiments already described, three instances of independent jaw action in birds possessing a well-developed postorbital ligament have come to my attention. Two of these represent jaw motions during yawning—one in the night heron (*Calherodias leuconotus*) observed by me (see p. 24) and the other described by Yudin (1958, p. 168), who gave the sequence of jaw motions in a gull as follows: (1) lower jaw maximally depressed, (2) upper jaw raised, (3) upper jaw lowered, and (4) lower jaw raised. The third instance appears in a series of photographs of the great snipe (*Capella media*) taken by P. O. Swanberg (1956). In these birds, protraction of the upper jaw is restricted to the tip of the bill, where it would be readily evident by comparison with the immovable base-line provided by the rest of the upper jaw. Several photographs show the closed bill and its slight downward curve. Plate 74 shows the lower jaw slightly open and in plate 73 quite widely open, but in neither case is there any change in the downward curve of the tip of the upper jaw and thus no protraction or coupling.

Jaw Articulation

One important question remains to be answered: how did the depressor mandibulae effect protraction in the evening grosbeak and in the domestic chicken after removal of the postorbital ligaments? In addition to coupling of the two jaws by the postorbital ligament, Bock (1964, p. 18) briefly referred to another type of coupling through an interlocking of the condyles of the quadrate and articular with the result that the mandible cannot be depressed without forward motion of the quadrates. He listed certain families of birds in which this interlocking is well or moderately developed, citing *Balaeniceps* as a prime example, but he offered no explanation of this action. Although neither of the species used for experiments in the present study is coupled through the jaw articulation to a high degree, a discussion of the mechanism in *Balaeniceps* will serve to introduce the general problems of coordination of the jaws through the jaw articulation.

In *Balaeniceps* (fig. 9), the quadrate has two main condylar surfaces, the inner of which (medial condyle) forms a double crest lying parallel to the plane of movement of the quadrate. The lateral condyle is somewhat curved, lying approximately perpendicular to the crest and to the plane of quadrate motion (its posteromedial

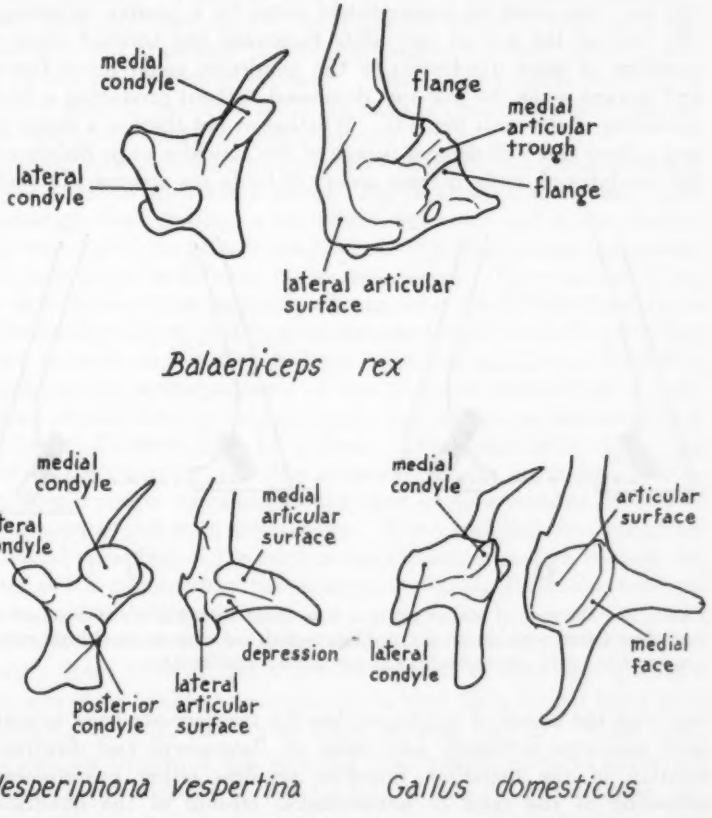


FIGURE 9.—Structure of jaw articulation in *Balaeniceps rex*, *Hesperiphona vespertina*, and *Gallus domesticus*. (Ventral view of right quadrate and dorsal view of left articular shown for each species.)

portion is expanded into a prominent condyle that is often referred to as the posterior condyle of the quadrate). These condyles fit into corresponding depressions or surfaces of the articular bone, and flanges on the upper edges of the medial articular trough grip the crests of the medial condyle of the quadrate, holding the articulated lower

jaw of a completely cleaned skull in place, as described by Böhm (1930) and others. Partly because of the gripping flanges but primarily because of the structure of the crests, trough, and lateral articular surfaces, the lower jaw can be depressed or raised only if the quadrate and articular surfaces slide along each other in the direction dictated by the crests and troughs. During depression of the jaw, this could be accomplished either by a passive spreading of the rami of the jaw as they slide backward and upward along the condyles of fixed quadrates; or the quadrates could move forward and inward while the jaw was depressed without producing a lateral spreading of the rami (fig. 10). Whether or not there is a flange grip and a deep and well-defined trough of the articular as in *Balaeniceps*, the condyles of many diverse orders of birds are arranged in such a

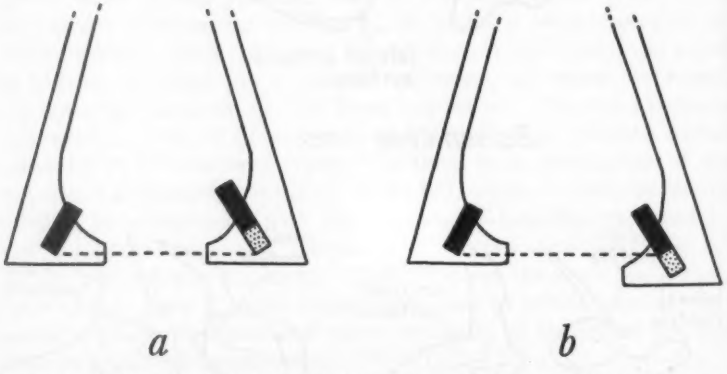


FIGURE 10.—Diagrams of relative positions from dorsal view of ramus of lower jaw and quadrate (black) when the jaw is closed (left ramus), and when depressed (right ramus): *a*, quadrate moves anteromedially; *b*, ramus moves posterolaterally.

way that the planes of motion within the two jaw-quadrate articulations converge anteriorly like those of *Balaeniceps* and downward rotation of the mandible therefore requires either posterolateral spreading of the rami or anteromedial motion of the quadrates. Protraction of the upper jaw thus will accompany depression of the lower jaw if resistance to spreading of the rami is greater than resistance to forward and inward rotation of the quadrates (which of course depends upon the combined resistance of all flexible portions of the upper jaw and palate). Protraction would be prevented if the quadrates were held in place, but depression of the lower jaw could still occur through spreading of the rami. Birds vary greatly in the ease of motion of the palate and upper jaw and in the lateral flexibility of the rami; the extent to which the rami may contribute to protraction

through the jaw articulation unfortunately has not been established for any species to my knowledge. Manger Cats-Kuenen (1961, pp. 18, 19) explained the coupling action of the jaw articulation in detail and concluded that independent motion of the two jaws in the hornbill *Rhinoplax vigil* was impossible because the rami had no lateral flexibility. I believe, however, that the flexibility necessary for independent depression of the mandible exists in *Rhinoplax* because even in a dried skull it is easy to depress the lower jaw by pressing on the retroarticular processes. When the kinetic mechanism is immobilized in the dried skull, the rami nevertheless readily spread apart during depression of the mandible.

It is probable that the conformation of the jaw-quadrate articulation played a role in protraction through the depressor mandibulae in the evening grosbeak (lacking a postorbital ligament) and in the chicken after removal of the postorbital ligament (fig. 4) although the mechanism appears to be different in the two species. The condyles of the jaw articulation of the domestic chicken are quite different from those of *Balaeniceps* (fig. 9), but both species have lateral surfaces providing broad support and medial surfaces providing guidance. In *Gallus domesticus* the medial condyle of the quadrate slides along a well-defined medial face (corresponding to the trough of *Balaeniceps*) of the broad, flattened articular surface. The medial faces of the two rami converge anteriorly. Depression of the lower jaw in the chicken, therefore, requires spreading of the rami or anteromedial motion of the quadrates just as in *Balaeniceps*. The possibility that resistance to lateral spreading of the rami in the chicken is enough to raise the upper jaw is suggested by the occurrence of protraction after removal of the postorbital ligaments.

The structure of the jaw articulation in the evening grosbeak differs sharply from that of the domestic chicken in that the quadrate possesses three knoblike condyles and in that the articular has a deep depression between its two articular surfaces (fig. 9). There is no well-defined trough of the articular that would serve to guide the motion of the rounded medial condyle of the quadrate; rather, the medial condyle rests on the top of a narrow medial articular surface that slopes downward and terminates just in front of the condyle when the jaws are closed. As the lower jaw is depressed, the medial and posterior condyles of the quadrate slide forward on the inclined surfaces of the articular to occupy the space or depression in front. With contraction of the depressor mandibulae, protraction appears to be caused by pressure of the articulation surfaces of the lower jaw on the quadrate condyles. The quadrate slides forward easily because of the slope of the articular surfaces.

Discussion

I have been concerned primarily with the functional properties of only one paired muscle as it acts within the kinetic systems of various species of birds (see fig. 11). The depressor mandibulae muscles serve principally to open the upper and lower jaws simultaneously. In most species the most powerful agents for protracting the upper jaw are undoubtedly the protractor quadrati et pterygoidei muscles, which

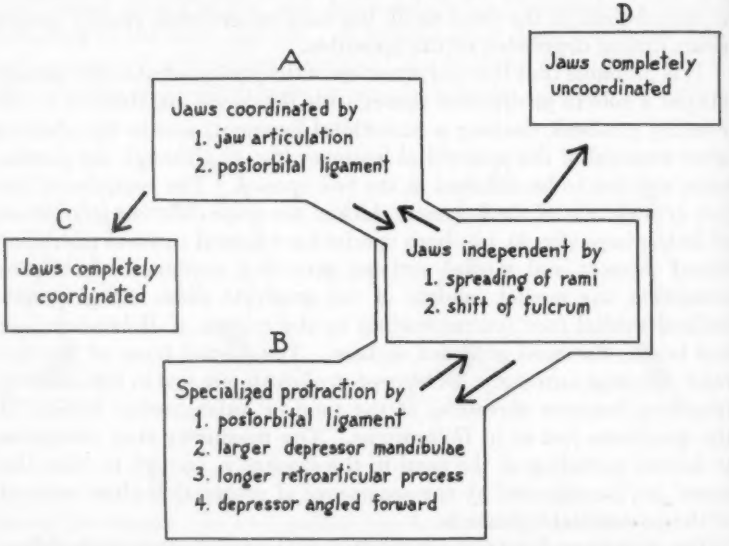


FIGURE 11.—Diagram of kinetic possibilities through the depressor mandibulae in the avian jaw: Species A has weakly coordinated jaws that may be moved independently. Species B has developed stronger protraction of the upper jaw through the mechanisms of coordination but can also overcome coordination. Species C has no capacity for independent jaw action, whereas species D has no coordination through the jaw-quadrate complex. (C and D are hypothetical.)

almost certainly come into play during maximum or forceful gaping. The depressor mandibulae, however, may be the sole or principal muscles opening both jaws when extensive or powerful opening of the jaws is not required, as in taking small food items from a substrate.

The mechanisms by which the depressor mandibulae can protract the upper jaw involve the angle of the muscle, the angle of sliding of the jaw-quadrate surfaces, the rigidity of the rami of the lower jaw and of the kinetic mechanism, the presence of a postorbital ligament or a comparable ligament, the length of the retroarticular process of

the mandible, the presence of ligamentous adductor muscles, and the resistance to depression of the lower jaw by environmental forces. Other features may be involved as well and a variety of factors probably contribute to jaw motion in each species. The mechanisms are developed to varying degrees in different groups of birds. Only by understanding their functional properties can we recognize convergence, independent divergent solutions to similar problems, and adaptive radiation in the kinetic mechanism. A survey of such trends in birds or in any group of birds has not yet been made in detail, but a few cases of variation in the depressor mandibulae complex should be mentioned here.

Certain birds that habitually probe into flowers or fruit show a combination of features that suggest a special role of the depressor muscles for protracting the upper jaw. Representatives of the "Coerèbidae" (*Coereba flaveola*), Zosteropidae (*Zosterops annulosa*), and Drepanididae (*Vestiaria coccinea*) display large depressor muscles, well-developed retroarticular processes of the mandible, and strong postorbital ligaments (Beecher, 1951a, pp. 277, 283; Moller, 1931, p. 126). Beecher (1951a, p. 285) states that "The Neotropical nectar-adapted tanagers are non-gapers. In none of them is *M. depressor mandibulae* more highly developed than in *Cyanerpes* . . . and it is apparent that these species simply insert the bill into flowers and sip nectar." Moller (1931, p. 110), however, illustrates *Dacnis cayana* as having a large depressor mandibulae, which, combined with its strong postorbital ligament, long retroarticular process, and relatively straight culmen and gonys strongly suggests that gaping is among its feeding patterns. Various members of the Icteridae display these same features and, in addition, have the depressor muscles angled well forward (Beecher, 1950, 1951b). Associated with this highly developed gaping adaptation is the straight culmen and gonys so characteristic of many icterids, essential for effective parting of the grass, earth, or flesh of a fruit with the outer edges of the bill. The starling (*Sturnus vulgaris*) is convergent with the icterids, especially *Sturnella*, in some features related to gaping but divergent in others (Zusi, 1959). Certain parrots have the depressor mandibulae muscles enlarged and strongly angled forward (*Nestor notabilis* and *Cyanorhamphus novae-selandiae*, illustrated in Hofer, 1950, pp. 457, 463). The retroarticular process is well developed but the postorbital ligament is lacking. Parrots are well known for their extraordinary mobility of the upper jaw, but no comparative information on this property in the Psittacidae is available. Among the probing Scolopacidae, the woodcock (*Scolopax*) shows special development of the depressor mandibulae and retroarticular process of the mandible (see Marinelli, 1928, fig. 8), possibly in relation to the need for

protraction in relatively firm earth. Galliform and anseriform birds display a long retroarticular process of the mandible but neither group has an obvious need for powerful depression of the lower jaw. Rather, the process may be related to kinetic action through the depressor mandibulae muscles.

The examples just given represent birds in which there is a need for strong, extensive, or repeated protraction and in which a combination of features associated with the depressor mandibulae is adapted to accomplish or to aid protraction. Other examples can be found among the passerine birds (see illustrations in Beecher, 1953, pp. 302, 318), but the elucidation of the adaptive radiation within these groups remains a challenge for the anatomist.

EVOLUTION OF THE INTERLOCKING JAW ARTICULATION.—Bock (1964, p. 37) postulated an obligatory coupling of the jaws through the postorbital ligament and thus found no explanation for the presence of two strict coupling mechanisms (postorbital ligament and jaw articulation) in the same species or for the evolution of jaw-articulation coupling. Explanations for these phenomena are possible, however, with the knowledge that coupling may be bypassed and that the postorbital ligament serves functions other than coupling. The fulcrum provided by the postorbital ligament causes the posterior portion of the depressed mandible to be rotated upward and forward. One result is that the mandible pushes the quadrates forward at least during the initial phases of depression, but another consequence is that a firm contact of the jaw and quadrate surfaces is assured throughout motions of the lower jaw. Without the postorbital ligament (or some functional equivalent) the anterior surfaces of the jaw articulation would tend to separate during depression of the mandible. As the condyles of the jaw articulation may serve to coordinate jaw motions, the ligament would enhance coordination by keeping the articulation surfaces in close apposition. The postorbital ligament could thereby play an important part in the evolution of the interlocking grooves and ridges of the jaw articulation. Support for the lower jaw through interlocking in a species such as *Balaeniceps* is lost quickly if the rami are spread slightly or the quadrates displaced anteromedially at any given position of the lower jaw, and it cannot be assumed that ligamentary supports are unnecessary in specialized "articulation-coupled" forms. The postorbital ligament is a structure that probably developed early in the evolution of modern birds and has played a role in the evolution of increased articulation-coupling in various groups while being reduced or lost in others. Its loss may be associated with the development of maximum independence of jaw motion.

FUNCTIONS OF KINESIS.—Bock (1964, pp. 25–31) discussed six possible functions of kinesis: (1) maintaining the mandible in the closed position, (2) gaping, (3) maintenance of the primary axis of orientation of the bill, (4) faster closing of the jaws, (5) more widespread and even distribution of jaw muscle attachment, and (6) shock absorbing. Of these, I believe that the first is doubtful because it requires the hypothesis of strict coupling of the jaws for its explanation and because the ligament does not hold the lower jaw closed (at least in *Gallus domesticus*). The third and sixth are probably of widespread importance—the third because many species rely on rapid grasping of tiny food items or of moving prey and the last because of the light construction of the jaws and palate in birds.

I believe that a primary advantage of kinesis is that it provides increased possibilities for diversity of manipulation by the jaws. Although birds lack teeth, they nevertheless must perform many manipulative tasks with the bill such as the capture, holding, orientation, manipulation, and swallowing of food, nest-building, preening, defence, and other activities. Two fundamental features of skull construction in birds serve, in combination with kinesis, to enhance the diversity of manipulation.

First, the tomial edges of the upper jaw are drawn forward when raised and backward when lowered (fig. 12*b*) because the flexible point of attachment of the upper jaw and cranium lies above the plane of the tomia. In most birds the articulation of the lower jaw lies below the tomial plane and there is a similar forward and backward motion of the tomium during depression and adduction of the lower jaw. A food item being constricted by the jaws, therefore, is wedged backward toward the throat rather than pushed forward as it would be by a straight pair of tongs (fig. 12*a*). Immobility of the upper jaw would reduce considerably this effect. Unfortunately, I can say nothing about its significance for the living bird although its existence can scarcely be doubted. The effect is greatest in relatively short and deep bills, where it may provide more effective seed-cracking forces or help to keep seeds from slipping forward in the bill during nibbling.

A second type of manipulation is made possible by the anterior placement of the flexible cranial attachment of the upper jaw relative to the articulation of the lower jaw (fig. 13). The upper jaw thereby rotates about a shorter radius than the lower, and the tomial edges can be opposed in a greater variety of ways than would be possible otherwise, especially if the upper jaw can be retracted below the resting position as discussed by Beecher (1951b, p. 413) and Yudin (1965, p. 68). Bock (1964, pp. 23, 24) argued against such retraction in a coupled skull, but I have shown here that coupling can be over-

come readily, at least in *Gallus domesticus*, and the theoretical objections to retraction of the upper jaw below the resting position thus are eliminated. While watching a night heron (*Calherodias leuconotus*) at close range in the New York Zoological Park, I observed retraction of the upper jaw when the bird was yawning. Just before

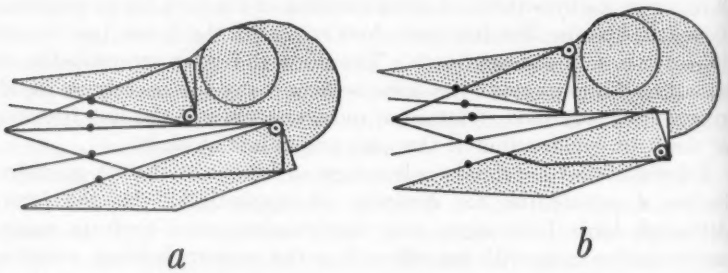


FIGURE 12.—Diagrams showing positions of tomial edges and of particular points (dots) on the tomia during motions of the two jaws: *a*, when centers of jaw rotation lie close to tomial planes; *b*, when centers of jaw rotation lie far from tomial planes.

FIGURE 13.—Diagram of the avian skull showing retraction of the upper jaw beyond the normal closed position. Because the lower jaw articulates well behind the cranial bending axis of the upper jaw, the manipulative possibilities of the jaw are increased. Biting with the bill tip as shown would not be possible if the jaws were of equal length.

raising the depressed mandible to its resting position, the bird retracted its upper jaw below the resting position with the result that only the tips of the jaws were touching and the gap between the bases of the jaws was clearly visible. Herons have the postorbital ligament well developed and are also "coupled" through the jaw-

quadrate articulation. It thus appears that retraction of the upper jaw beyond the resting position is one of the capabilities of avian kinesis. Its importance lies in the potential for increased diversity of manipulation by the bird's beak.

In studying the functional significance of the palatine process of the premaxilla, Bock (1960) postulated that there are two methods of seed-cracking used by heavy-billed finches. The first he called "the nutcracker method," characterized by a kinetic upper jaw and equal development of the adductors of the mandible and the retractors of the palate. He ascribed this method to the emberizine finches and richmondenine finches. By contrast he claimed that the cardueline finches employ "the vise method," which he describes (p. 427) as follows:

> In the specialized carduelines, the upper jaw has lost its mobility; it is a nearly stationary block against which the mandible presses. Heavy bosses of bone (the lateral flanges) and rhamphotheca distribute the shocks associated with the cracking of the seed evenly to all parts of the braincase. Only the adductor muscles are well developed in the cardueline finches; in fact, the muscles associated only with the movement of the upper jaw have become small and are on the verge of becoming functionless.

We have seen that the evening grosbeak—one of the heavy-billed cardueline finches—has a kinetic upper jaw that operates even in the absence of contraction by its prime protractors, the *M. protractor quadrati et pterygoidei*. In order to exert a seed-cracking force, the upper jaw must be moved in opposition to the adduction of the lower jaw or held stationary while force is exerted by both jaws, requiring in either case a powerful *M. pterygoideus*. It thus seems doubtful that the vice and nutcracker methods of jaw action are of general validity although certain species may have become specialized in one direction or the other (e.g., *Coccothraustes* [Sims, 1955]). Kinesis may be important to seed-cracking forms for manipulation of seeds and for the application of biting forces from different angles as explained above.

The role of the depressor mandibulae in avian kinesis can at present only be inferred from a knowledge of its functional-anatomical properties. My findings suggest that through linkages of various kinds the depressor mandibulae may serve to open both jaws simultaneously when strong protraction is not required, whether or not a postorbital ligament is present. In those species with a strong postorbital ligament and/or interlocking condyles of the jaw articulation and especially in those in which the muscle angles far forward from its insertion and in which the retroarticular process of the mandible is well developed, the depressor may have a more precise and powerful effect in opening both jaws. Further investigations of these problems through comparative morphology, physiology, and behavior may be

expected to broaden our understanding of structural diversity in the avian skull.

Summary

Experiments on the action of *M. depressor mandibulae* in *Gallus domesticus* and *Hesperiphona vespertina* demonstrate that the muscle causes protraction of the upper jaw as well as depression of the mandible. The coordination of both jaws is enhanced by the presence of a postorbital ligament and/or by modifications of the jaw-quadrate articulation. The mechanism of protraction through the postorbital ligament and depressor mandibulae is explained through force analysis and it is shown that the force and amount of protraction vary with muscle angle and length of the retroarticular process of the mandible. Independence of jaw motion may be achieved by a backward shift of the mandible or by spreading of the mandibular rami. The role of the postorbital ligament in the evolution of coordination of the jaws through the jaw articulation is presented. Two general properties of avian skull structure are shown to diversify the manipulative capabilities of the bill in a kinetic skull.

Literature Cited

BARNIKOL, A.

1952. Korrelationen in der Ausgestaltung der Schädelform bei Vögeln. Morph. Jahrb., vol. 92, pp. 373–414.

BEECHER, WILLIAM J.

1950. Convergent evolution in the American Orioles. Wilson Bull., vol. 62, pp. 50–86.

1951a. Convergence in the Coerebidae. Wilson Bull., vol. 63, pp. 274–287.

1951b. Adaptations for food-getting in the American Blackbirds. Auk, vol. 68, pp. 411–440.

1953. A phylogeny of the oscines. Auk, vol. 70, pp. 270–333.

BOCK, WALTER J.

1960. The palatine process of the premaxilla in the Passeres. Bull. Mus. Comp. Zool., Harvard, vol. 122, pp. 361–488.

1964. Kinetics of the avian skull. Journ. Morph., vol. 114, pp. 1–41.

BÖHM, M.

1930. Über den Bau des jugendlichen Schädels von Balaeniceps rex nebst Bemerkungen über dessen systematische Stellung und über das Gaumenskelet der Vögel. Zeit. Morph. Ökol. Tiere, vol. 17, pp. 677–718.

HOFER, HELMUT

1950. Zur Morphologie der Kiefermuskulatur der Vögel. Zool. Jahrb., Anat. Ont. Tiere, vol. 70, pp. 427–556.

KALKOFEN, ULRICH P.

1963. Effect of *M. depressor mandibulae* on the upper jaw in birds. Unpubl. senior honors thesis in zoology, University of Maine.

KRIPP, DOMINIK V.

1933. Beiträge zur mechanischen Analyse des Schnabelmechanismus. Morph. Jahrb., vol. 72, pp. 541–566.

MANGER CATS-KUENEN, CHARLOTTE S. W.

1961. Casque and bill of Rhinoplax vigil (Forst.) in connection with the architecture of the skull. Verh. Kon. Nederlandse Akad. Weten., vol. 53, pp. 1–51, 12 figs.

MARINELLI, W.

1928. Über den Schädel der Schnepfe. Palaeobiologica, vol.1, pp. 135–160, 1 pl.

MOLLER, WALTER

1931. Über die Schnabel-und Zungenmechanik blütenbesuchender Vögel, II. Biologia Generalis, vol. 7, pp. 99–154.

SIMS, R. W.

1955. The morphology of the head of the hawfinch (*Coccothraustes coccothraustes*). Bull. British Mus. (Nat. Hist.), vol. 2, pp. 369–393.

STARCK, D.

1940. Beobachtungen an der Trigeminus-muskulatur der Nashornvögel nebst Bemerkungen über einige Besonderheiten des Vogelschädels und über die Kiefermuskulatur in allgemeinen. Morph. Jahrb., vol. 84, pp. 585–623.

SWANBERG, P. O.
1965. Studies of less familiar birds, 138: Great Snipe. British Birds, vol. 58, pp. 504–508, 8 pls.

YUDIN, K. A.
1958. Skull kinesis of Lari and Alcae. Acad. Sci. U.S.S.R., Trudy Zool. Inst., vol. 25, pp. 164–182. [Translated from Russian.]
1965. The phylogeny and classification of the Charadriiformes. Acad. Sci. U.S.S.R. Zool. Inst., new series, no. 91. Fauna of the U.S.S.R., Birds, vol. 2, no. 1, pt. 1, 260 pp. [Translated from Russian.]

ZUSI, RICHARD L.
1959. The function of the depressor mandibulae muscle in certain passerine birds. Auk, vol. 76, pp. 537–539.
1962. Structural adaptations of the head and neck in the Black Skimmer, *Rynchops nigra* Linnaeus. Publ. Nuttall Orn. Club, no. 3, 101 pp.

U. S. GOVERNMENT PRINTING OFFICE: 1967

VOL. 123

tish Birds,

rudy Zool.

Acad. Sci.
e U.S.S.R.,
ssian.]

n passerine

Skimmer.
3, 101 pp.

CE: 1967